

## 6. THE ECOLOGY OF ESTABLISHMENT

P. J. GRUBB

*Botany School, University of Cambridge, CB2 3EA*

### SUMMARY

Approaches to the study of plant establishment in the context of landscape design are briefly reviewed, and three issues are considered in more detail: the diversity of pioneers in relation to substratum type, the rarity of pioneer plants with nitrogen-fixing symbionts in relation to the increase in rooting density during succession, and the frequent importance of 'third parties' in controlling the balance between any two plants during establishment in gaps in an already complete vegetational cover. Examples of third parties are birch trees tipping the balance between two fir species during regeneration in a subalpine forest, voles making gaps in a heath layer in which birches may regenerate, and mycorrhizal fungi having favourable effects on some species of short-lived plants and deleterious effects on others.

### INTRODUCTION

There are two kinds of working situation in which an ecologist may be confronted with landscape design. First, he may have to advise on the establishment of vegetation on totally bare sites. Secondly, he may have to draw up a scheme for the management of an area with a complete vegetational cover, where some species are to be encouraged, others introduced and yet others ousted. A sound understanding of the ecology of establishment of different sorts of plants is essential for landscape design in both the first case (which we may call 'constructive') and in the second case (which we may call 'manipulative').

Among ecologists working with natural and semi-natural vegetation, much less attention has been paid to landscapes newly available to plants than to landscapes with a vegetation cover, albeit often subject to massive disturbance by fire, flood, windthrow or man's activities. Wherever ecologists have studied in detail the dynamics of vegetation, they have found that every plant species present has slightly different requirements for the best chance of producing a new adult individual. The differences between species concern the conditions that are most favourable for flower-formation, pollination, seed-set, dispersal, germination, establishment and onward growth; an extensive

review of this issue was provided not long ago (Grubb 1977). More recently, accounts emphasizing the different kinds of natural disturbance that favour particular species have been published for example, by White (1979), Pickett (1980) and various authors in the volume edited by West *et al.* (1981). A valuable alternative approach to the study of establishment has been the abstraction of major characteristics of whole groups of species with similar requirements. For example, Wells (1976) and Bazzaz (1979) have reviewed the differences in morphology and physiology between early successional and late successional species on forest clear-cuts and abandoned fields in the eastern USA, and Grime has produced his C-S-R model (see Chapter 11).

In the present paper I cannot attempt a comprehensive review, and instead I shall develop just three generalizing themes which have, in my opinion, received insufficient attention: (i) the diversity of pioneers that is to be understood in relation to the type of substratum colonized; (ii) the general failure of vascular plants with symbiotic nitrogen-fixing micro-organisms to be pioneers; and (iii) the frequent importance of 'third parties' (other plants, animals or micro-organisms) in determining the balance between any two plant species during establishment.

#### DIVERSITY OF PIONEERS IN PRIMARY SUCCESSION

A primary succession is said to occur where there is long-term directional change in the composition of the plant cover on a site initially devoid of vegetation and without a developed soil. A 'pioneer,' in the strict sense, is one of the first plants to become established at a particular site; to be effective it must also be able to continue development to the stage of reproductive adult. 'Establishment' is taken to mean the attainment of a recognizable juvenile vegetative stage; it is not possible to be more precise without referring to the type of plant concerned (lichen, moss, tree, herb, etc.). Pioneers may be transitory or persistent; their essential feature is their ability to become established before other plants.

I shall confine myself to plants which are pioneers on relatively stable terrestrial sites; the special problems of pioneers on screes and sand dunes, salt marshes and lake edges are reviewed by Ellenberg (1982). The kind of landscape which has been open to pioneer plants on much the largest scale in the last million years is that which has been newly freed from glacial cover, and it is convenient to start by considering the pioneers found these days where a long glacial tongue has retreated from well within the range of present-day forest. Examples of such landscapes have been described for western North America (Cooper 1916, 1923), Scandinavia (Faegri 1933), the European Alps (Richard 1975) and New Zealand (Wardle 1980). In parallel with the range of

topographic site-types we find a remarkable range of pioneers (Fig. 6.1) with distinctive distributions (Fig. 6.2). Little precise information is available on their physiological characteristics, but a tentative analysis is included in Fig. 6.2. The growth rate is consistently inversely proportional to the length of life, but the relationship between final size and length of life is more complicated as (in general) the smallest live longest, the tallest next longest and the plants of intermediate size live the shortest time.

Among the pioneers, the growth form and growth rate match the capacity of the substratum to supply water and mineral nutrients. I suggest that the differentiation of plant types may have more to do with nutrient supply than water supply. Of particular interest is the differentiation between trees and herbs. There is increasing evidence that in forested country in more mature landscapes an abundance of herbs in the field layer is characteristic of relatively nutrient-rich sites, and an abundance of shrubs and young trees is characteristic of relatively infertile soils, and this is true of both dry areas (where the herbs are often grasses) and moist areas (where they are usually broad-leaved dicotyledons). References are given by Grubb (1984).

The relationship between the type of pioneer and the type of substratum shown in Fig. 6.2 applies not only to deglaciated landscapes but also to landslip scars, large outcropping rock-formations, and volcanic debris. The importance of a comparatively poor nutrient supply in favouring trees as pioneers is clearly brought out by considering the plants of landslip scars in the wetter regions of the world. It is often seen that trees are pioneers on the rockiest parts of the scars, where the nutrient supply is poorest, while faster-growing shrubs and herbs are found on the mixed debris at the lower ends of the landslips. Wardle (1980) has described how, in the Westland of New Zealand where the annual rainfall is up to 5000 mm and there is no dry season, the trees *Metrosideros umbellata* and *Weinmannia racemosa* are the pioneers on upper, rocky parts of landslips, while shrubs such as *Coprosma rugosa* and *Hebe salicifolia* are the pioneers on the lower parts composed of rock debris including a certain amount of fine earth. Trees can also be the pioneers on bare rock in seasonally dry climates, like *Oedomatopus ovata* on the convex surfaces of granite 'Inselbergen' in the Orinoco basin, where various drought-tolerant herbs (including the strange *Vellozia tubiflora*) are the pioneers on ledges where weathered rock accumulates, and where grasses dominate on the deepest soil-accumulations (P.J. Grubb, pers. obs.).

In Japan, lavaflows and 'mudflows' (often including aggregations of huge rocks) are widespread and very varied in texture. Yoshioka (1974) has emphasized that trees and shrubs are the usual pioneers at rocky sites, and has illustrated the contrast with fine-textured mudflows on which grasses form a closed cover that impedes establishment of woody plants.

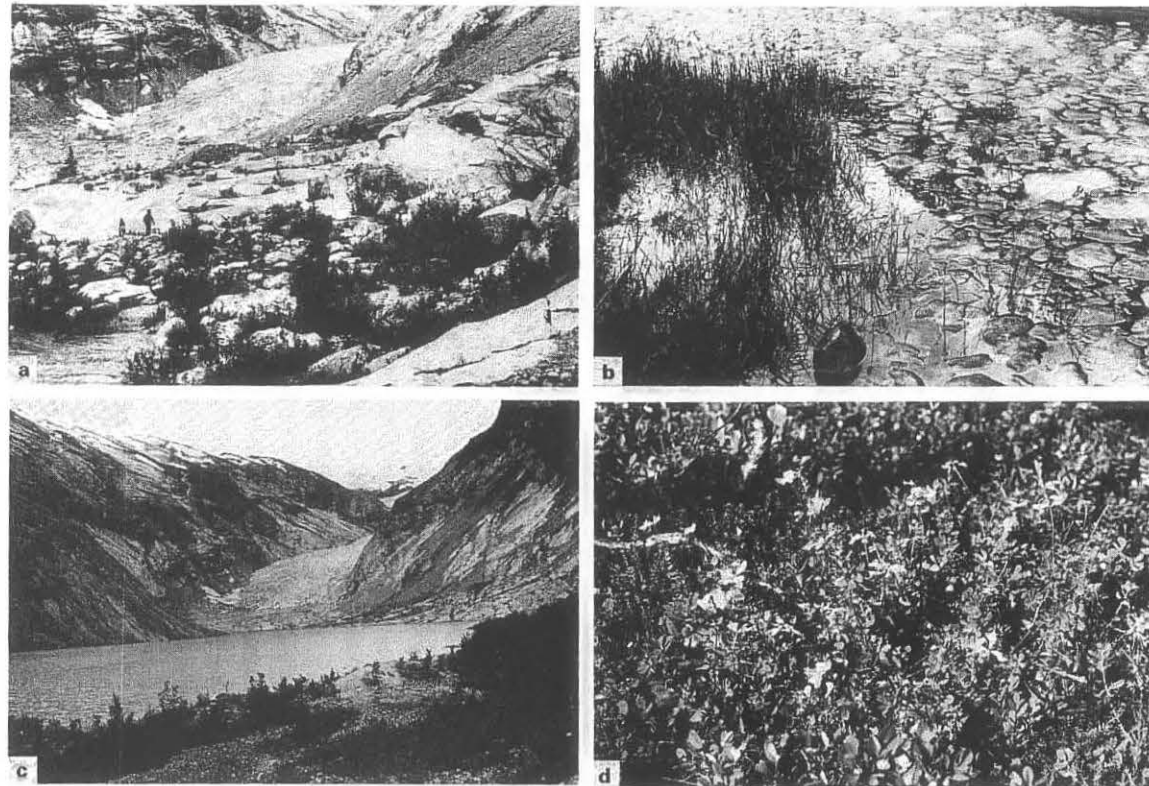


FIG. 6.1. (a) Area beneath snout of the Nilgarbreen Glacier in Norway in August 1983, with a little morainic material and much bare rock. *Salix* species (with mosses) were the major pioneers in rock crevices, while grasses (with mosses) were the major pioneers on gravel and silt. (b) Grasses as the major pioneers on fine-grained material at the margin of a small lake (with floating ice in August), a little further from the glacier than the foreground of (a). (c) Moraine further from the glacier than the foreground of (a), showing mixture of woody and herbaceous plants in developing birch-wood. Note the dark crowns of the nitrogen-fixing *Alnus incana* to the right, characteristically larger (faster-growing) than *Betula* or *Salix* but not a pioneer. (d) The major herb with nitrogen-fixing symbionts, *Lotus corniculatus*, in the succession at Nilgarbreen; characteristically found from mid- to late-successional stages, and not as a pioneer.

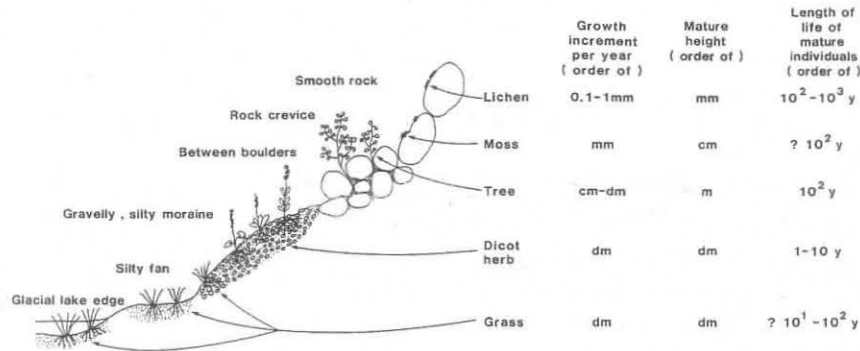


FIG. 6.2. The types of pioneer plant characteristic of different types of substratum in a recently deglaciated area within the range of present-day forest, and selected properties of the plants.

In fact, many different kinds of trees have been described as pioneers of rocky landslip sites in temperate and tropical regions, e.g. in Chile *Nothofagus* spp. (Veblen & Ashton 1978), in the Himalayas *Pinus* spp. (Stainton 1972), in Malaya *Macaranga* spp. (Whitmore 1975), and in Central and much of northern South America *Cecropia* spp. (Cuatrecasas 1958). In North America, trees such as *Betula papyrifera* have been described as pioneers on both large-block talus slopes (Cooper 1916) and on the rockiest parts of landslip-scars (Flaccus 1959), and in Norway *Betula* spp. can be seen behaving similarly on talus. Because talus slopes and landslips are rare in Britain it is in abandoned quarries that we most often see trees as pioneers—usually species of *Salix*, *Betula* or *Quercus*.

I do not mean to suggest that all woody pioneers can tolerate nutrient-poor sites. In fact, many are characteristic of sites with an abundance of fine earth. Such trees and shrubs may be found all the way from the lowlands of the tropics, e.g. *Eucalyptus deglupta* and *Octomeles sumatrana* in Papua New Guinea (Whitmore 1975), to the mountains of the temperate zone, e.g. *Myricaria germanica*, *Hippophae rhamnoides* and *Alnus incana* in the European Alps (Ellenberg 1982).

Contrasting strongly with pioneer trees of nutrient-poor sites are the fast-growing herbaceous pioneers of drift lines along the sea shore and along major rivers. They are peculiar 'pioneers' in that they are never followed by a second wave of invaders because each year the old drift is washed away and a new lot of drift is deposited; their communities are thus 'Dauer-Pioneer-Gesellschaften' (Tüxen 1975). Examples for the Rhine and its tributaries are given by Lohmeyer (1971) and summarized by Ellenberg (1982). They include many of

the herbs found these days in fertilized fields, on roadsides and in other nutrient-rich habitats, e.g. species of *Chenopodium*, *Matricaria*, *Papaver* and *Polygonum*. In contrast, the tree species of rocky landslip scars spread characteristically to road cuttings and fields that have been abandoned because of their infertility (cf. Whitmore 1975).

I suggest that the correct world perspective is to see trees as generally the pioneers of sites with more than enough mineral nutrients for lichens and bryophytes but insufficient for herbs. Where the growing season is too short and/or the temperatures are too low to support woody plants, then the pioneers at the corresponding sites are probably mostly bryophytes.

The physiological basis for the advantage of woody plants over herbs on nutrient-poor sites is only partially understood. It has long been known that woody plants tend to have lower maximum relative growth rates than herbs (Coombe 1960), and that this means that woody plants are prone to be eliminated by interference from herbs on more fertile sites. The lower relative growth rates result from lower maximum photosynthetic rates in the leaves (Jarvis & Jarvis 1964), and these may be linked to greater mean life-lengths for leaves on woody plants (cf. Orians & Solbrig 1977). I have suggested elsewhere (Grubb 1984) that the longer leaf-life may involve the use of a greater proportion of the leaf's nitrogen in 'defence' so that less is available for production of photosynthetic machinery.

The maximum development of dicotyledonous herbs on sites supplying somewhat less nutrients than those occupied by grasses, shown in Fig. 6.2, is also probably an observation that can be widely generalized. It is a fact that the nitrogen-starved 'Xerobrometum' communities of Central Europe often lack grass (*Carex humilis* taking its place; Ellenberg 1982), and the failure of grasses (as opposed to various shrubs, dicotyledonous herbs, orchids and sedges) to become established on extremely chalk-rich ex-arable in southern England as a result of nitrogen-shortage was elegantly demonstrated by Lloyd & Pigott (1967). Of course there are bound to be exceptions; *Sesleria albicans* is the most convincing case of a pioneer grass able to withstand severe nitrogen shortage in northern Europe (Dixon 1982). The physiological basis for the advantage of dicotyledonous herbs (and certain grass-like plants such as *Carex* spp.) over grasses on nitrogen-poor sites is for the moment unknown.

#### RARITY AMONG PIONEERS OF PLANTS WITH NITROGEN-FIXING SYMBIONTS

It is generally accepted that even the most favourable of the microhabitats shown in Fig. 6.2 is short of nitrogen (Lawrence 1958), and yet it is

characteristic of deglaciated landscapes that the vascular plants with nitrogen-fixing symbionts are not among the pioneers, but among the second or third wave of invaders, e.g. the legumes *Astragalus* and *Hedysarum* in North America (Viereck 1966) and *Lotus* and *Trifolium* in Europe (Ellenberg 1982), species of *Alnus* and *Dryas* in both continents (Cooper 1923; Faegri 1933; Viereck 1966; Ellenberg 1982), and *Carmichaelia* and *Coriaria* in New Zealand (Wardle 1980). On recent moraines on tropical mountains there are commonly no vascular plants known to have nitrogen-fixing symbionts; this is apparent from the accounts of Hedberg (1968) for East Africa and Hope (1976) for West Iran, and is also true of the Andes (P.J. Grubb, pers. obs.). However, it is possible that many pioneer vascular plants have effective parasymbiotic nitrogen-fixers in the rhizosphere, as is believed by some to be the case for marram grass (*Ammophila arenaria*) on dunes (Huiskes 1979). Shortage of nitrogen seems to be particularly severe for a group of pioneers not so far considered—epiphytes (Grubb, Flint & Gregory 1969; Grubb & Edwards 1982). In their case there is evidence that the shortage of nitrogen is slightly relieved through significant nitrogen-fixation by free-living micro-organisms in tree crowns (Jones *et al.* 1974), and by related organisms associated with epiphytic bryophytes (Edmisten 1970).

I suggest that the most probable explanation for the common failure of plants with nitrogen-fixing symbionts to be pioneers is that it is impossible to produce an exceedingly light and outstandingly dispersible seed which also contains sufficient 'starter nitrogen.' It is well established that the nitrogen capital in the relatively large, nitrogen-rich seeds of legumes is needed for investment in nodule-formation before any net return of nitrogen accrues to the angiosperm partner, and that the establishment of leguminous plants is often nitrogen-limited (Sprent & Thomas 1984). Other possible explanations could be a need for an increased phosphate-supplying power to develop in the soil by weathering (many legumes are strongly promoted by addition of phosphate), or a low probability of invasion together by vascular plant and symbiont. The two latter explanations seem less probable as there are a few cases where legumes are found as pioneers, e.g. *Astragalus alpinus* on base-rich till eroded by river action in northern Sweden, and *Lupinus densiflorus* var. *aureus* on steep roadside banks in the Coastal Range of California (P.J. Grubb, pers. obs.). In such cases the pioneers invade over distances of only a few metres, and the sites invaded are often below the source of seed.

A quite different approach to the problem is to suggest that a plant with nitrogen-fixing symbionts comes to have a strong competitive advantage only when the rooting density has reached a rather high value, and the effective shortage of nitrogen has increased relative to other limiting factors. Nitrate is highly mobile in the soil (Nye & Tinker 1977) and it can be taken up by any



given root from a large volume of soil around it. In contrast phosphate, also in short supply in most raw soils, is immobile and can be taken up from only a narrow sleeve of soil around each root. A simple way of showing the increasing importance of nitrate-limitation relative to phosphate-limitation as rooting density increases is to grow plants at the rate of one per large pot of soil, and to use soil which is (in general terms) low in both nutrients; additions of the nutrients are then made to separate plants. At least with some species it is found that at first only phosphate-addition will increase growth, and later only nitrate-addition (Fig. 6.3). It can easily be shown that this result is

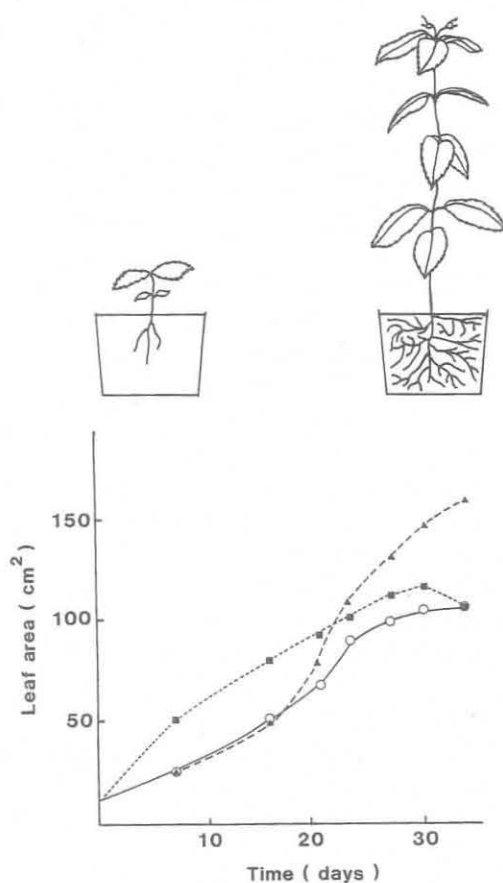


FIG. 6.3. Two stages in the development of a plant in a pot of soil, and the change-over with time from phosphate-limitation to nitrate-limitation; based on results of Peace & Grubb (1982) for *Impatiens parviflora* grown on a woodland soil derived from calcareous boulder clay. ○, no addition; ■, phosphate added; ▲, nitrate added.



dependent on rooting density and not on some other time-dependent factor by growing plants at a high rooting density from the beginning, e.g. ten in a small pot; then nitrate limits growth from the start (Peace & Grubb 1982).

The time is ripe for a critical investigation of the nitrogen relations of natural pioneers, and particularly the importance of nitrogen-shortage relative to other limiting factors at the pioneer stage and in the later phases of succession.

### IMPORTANCE OF THIRD PARTIES IN DETERMINING THE BALANCE BETWEEN COMPETITORS DURING ESTABLISHMENT

#### *Other plants as third parties*

Weatherell (1957) was one of the first to illustrate the importance of the third party during establishment, when he showed that *Calluna vulgaris* was able to suppress severely establishment of *Picea sitchensis* but not ~~of~~ that of *Larix leptolepis* in the Scottish uplands. An even more arresting example in a wholly natural system has been found by Kohyama (1984) in an area of Japanese subalpine forest, a part of which is subject to wave-patterns of regeneration driven by wind (Fig. 6.4). The two most abundant trees are species of *Abies*, both relatively shade-tolerant, but one (*A. mariesii*) more shade-tolerant and slower-growing than the other (*A. veitchii*). Where a windthrow area is created, leaving advanced growth of the two *Abies* spp. exposed, and there is no invasion by *Betula*, the less shade-tolerant *Abies* outgrows the other and forms a majority of the trees in the forest regenerated on the site. But if *Betula* invades, it grows faster than either of the *Abies* spp. and forms a mixed canopy with the *Abies* species. This mixed canopy tends to break up in an irregular fashion. Under these conditions the more shade-tolerant *Abies* species is favoured; it builds up a 'sapling bank' as opposed to a 'seedling bank', and individuals eventually grow up through the broken canopy. The frequency of invasion of gaps by *Betula* is such that the mean proportion of the more shade-tolerant *Abies mariesii* in the canopy over a wide area is about 0.6; without the intervention of the *Betula* it would certainly be rarer, and might be eliminated.

#### *Animals as third parties*

Remmert (1984) has emphasized the role of animals in controlling the balance between plant species in many kinds of landscape. A striking case that I recently studied was in northern Sweden near Abisko (68°N). The subalpine forest there has one principal tree species, *Betula pubescens* ssp. *tortuosa*

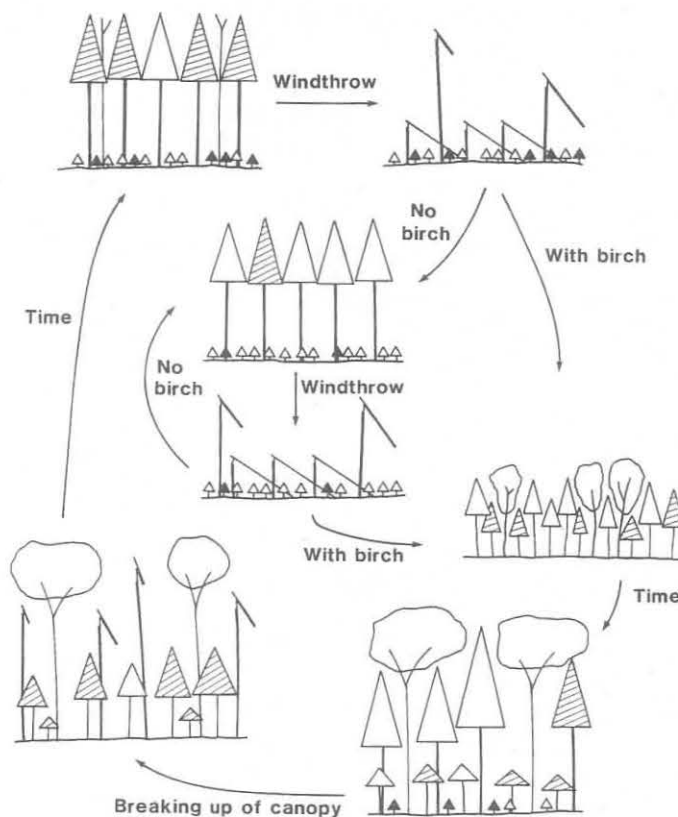


FIG. 6.4. A diagrammatic representation of the two major routes of regeneration in a subalpine forest in Japan studied by Kohyama (1984). The conifers with filled crowns are *Abies mariesii* (more shade-tolerant), those with open crowns are *A. veitchii*, and the broad-leaved trees are *Betula ermanii*.

(Rune 1965), and this forms multi-stemmed individuals that may be very long-lived. On acidic soils the field layer is composed of a dense 10-cm tall growth of *Empetrum hermaphroditum* and *Vaccinium* spp., in which seedlings of *Betula* cannot become established. However, every few years there are eruptions in the local populations of the vole *Clethrionomys ruficanus*, and areas of 0.5–4 m<sup>2</sup> in the heathy field layer are destroyed (Callaghan & Emanuelsson 1985). It seems that only in these gaps can the birch regenerate (Fig. 6.5).

#### *Micro-organisms as third parties*

It is a striking fact that very few species of short-lived plants can maintain populations in continuous short turf on chalk-derived soils in northern

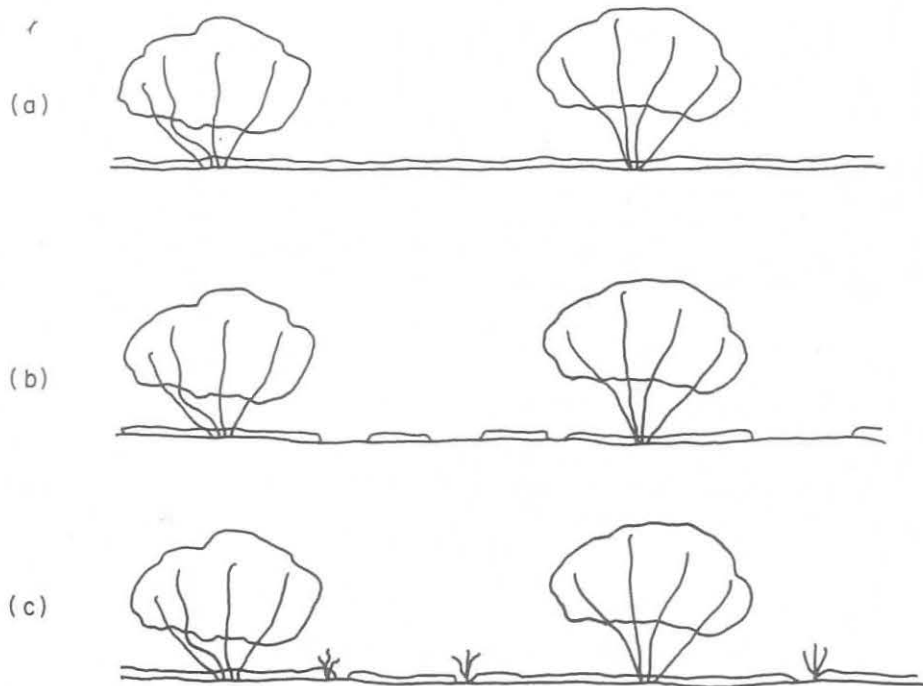


FIG. 6.5. Profiles of a relatively open, ridge-top facies of heath-type subalpine birch forest in northern Sweden, showing the creation of gaps by voles, and the apparent dependence of birch on these gaps for regeneration.

Europe, even when the turf is grazed to a height of only 2–10 cm. Common annual and biennial 'weeds', if sown into such turf, germinate but fail to become established (Gay *et al.* 1982). Fenner (1978) showed experimentally that common colonists of bare ground are highly susceptible to below-ground interference. He made gaps in an artificial sward of *Festuca rubra* kept to a height of 1 cm by regular cutting, and sowed various species; the colonists failed to grow where turf-inhabiting perennials succeeded in becoming established (Fig. 6.6). At least for *Arenaria serpyllifolia* addition of phosphate (but not nitrate) will relieve seedlings of the inhibition by a dense grass turf (P.J. Grubb, unpubl. data). It is therefore of particular interest that the most widespread biennials of chalk turf (*Linum catharticum* and various *Gentiana*-ceae) have peculiar mycorrhiza (Gay *et al.* 1982), almost certainly involved in phosphate uptake (Harley & Smith 1983). Taylor (1982) has shown experimentally that one of the *Gentianaceae* concerned (*Centaureum erythraea*) is very strongly dependent on mycorrhizal infection for development. Even more remarkable, she found in the same experiment that infection of nearby

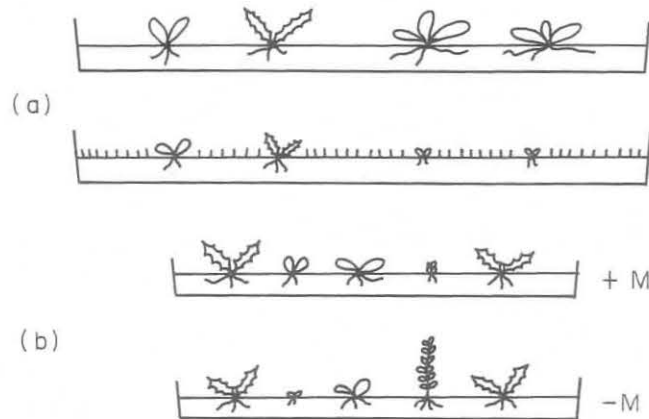


FIG. 6.6. Diagrams of (a) the experiment of Fenner (1978) showing differential suppression of 'turf-incompatible' plants, and (b) the experiment of Taylor (1982) showing differential effects of mycorrhizally infected inoculum plants on seedlings of various species grown in sterilized calcareous sandy soil.

'inoculum' plants of *Centaureum erythraea* and *Leontodon hispidus* with mycorrhiza caused a dramatic reduction in the growth of seedlings of the 'turf-incompatible' *Arenaria serpyllifolia* and *Verbascum nigrum* (Fig 6.6). It has yet to be proven that mycorrhiza can tip the balance in the field, and not merely under laboratory conditions, but the results are highly suggestive.

The issue of 'turf-compatibility' concerns not only short-lived herbs but also shrubs and trees. For example, in northern Europe and in the eastern United States species of *Crataegus* are especially effective in invading derelict grassland, whereas species of *Cornus* and *Viburnum* are very effective in invading bare soil left after arable cultivation, or where rabbits have had their burrows. The late P.S. Lloyd suggested that differences in root morphology were of key importance in this context (Ellenberg 1982) but I suspect that the nutrient relations of the whole plant and the mycorrhizal type, may well prove to be of equal importance.

#### CONCLUSIONS FOR LANDSCAPE DESIGN

Natural pioneers are enormously varied, and much of this variation can be related to the extent of the nutrient supply. Of particular interest, not least in the applied context, is the balance between trees and herbs. If, for example, it is desired to cover motorway cuttings with trees, it might be better not to cover the slopes with fertile topsoil which will encourage the growth of grasses that

can suppress any trees that are planted, but to plant trees (or scatter seeds) on the infertile subsoil and so save a good deal of money.

Legumes and other plants with nitrogen-fixing symbionts are undoubtedly important in encouraging growth of plants in young systems on infertile soils, e.g. conifer plantations on old sand dunes, but the nitrogen relations of the very earliest stages in primary succession, as in old chalk-pits and other quarries, need to be re-examined critically.

Species of later stages in succession differ among themselves, not only in their requirements regarding physical aspects of the environment which are relatively easily measured, e.g. temperature and moisture supply, but also in the degree to which their juveniles are dependent on third parties for successful establishment. This element of dependence is important naturally in determining which species can grow in a community and their relative abundance. Therefore, if it is desired to manipulate a landscape, and change the balance of species, the inter-relations between the juveniles of those species and various third parties in the ecosystem should be considered most critically.

#### ACKNOWLEDGMENTS

I am particularly indebted to Drs T.V. Callaghan, U. Emanuelsson and T. Kohyama for showing me their papers before publication, and to Dr Pamela Taylor (née Gay) for permission to quote her unpublished results; her research was supported by the Natural Environment Research Council. I thank Professor P.W. Price (Northern Arizona University) for encouraging my interest in the importance of 'third parties'.

#### REFERENCES

- Bazzaz, F.A. (1979). The physiological ecology of plant succession. *Annual Reviews of Ecology and Systematics*, **10**, 351–371.
- Callaghan, T.V. & Emanuelsson, U. (1985). Population structure and processes of tundra plants and vegetation. *The Population Structure of Vegetation* (Ed. by J. White), pp. 399–439. Junk, Dordrecht.
- Coombe, D.E. (1960). An analysis of the growth of *Trema guineensis*. *Journal of Ecology*, **48**, 219–232.
- Cooper, W.S. (1916). Plant successions in the Mount Robson region, British Columbia. *Plant World*, **19**, 211–238.
- Cooper, W.S. (1923). The recent ecological history of Glacier Bay, Alaska. *Ecology*, **4**, 93–128, 223–245, 355–365.
- Cuatrecasas, J. (1958). Aspectos de la vegetación natural de Colombia. *Revista de la Academia de Ciencias Naturales de Colombia*, **10**, 221–262.
- Dixon, J.M. (1982). Biological Flora of the British Isles: *Sesleria albicans* Kit. ex Schultes. *Journal of Ecology*, **70**, 667–684.
- Edmisten, J.A. (1970). Preliminary studies on the nitrogen budget of a tropical rain forest. *A Tropical Rain Forest* (Ed. by H.T. Odum & R.F. Pigeon), pp. H-211–H-215. US Atomic Energy Commission, Oak Ridge, Tennessee.

- Ellenberg, H. (1982). *Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht*, 3rd edn. Ulmer, Stuttgart.
- Faegri, K. (1933). Über die Längenvariationen einiger Gletscher des Jostedalsbre und die dadurch bedingten Pflanzensukzessionen. *Bergens Museums Årbok*, 1933 (7), 1–255.
- Fenner, M. (1978). A comparison of the abilities of colonizers and closed-turf species to establish from seed in artificial swards. *Journal of Ecology*, 66, 953–963.
- Flaccus, E. (1959). Revegetation of landslides in the White Mountains of New Hampshire. *Ecology*, 40, 692–703.
- Gay, P.E., Grubb, P.J. & Hudson, J.H. (1982). Seasonal changes in the concentrations of nitrogen, phosphorus and potassium, and in the density of mycorrhiza, in biennial and matrix-forming perennial species of closed chalkland turf. *Journal of Ecology*, 70, 571–593.
- Grubb, P.J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, 52, 107–145.
- Grubb, P.J. (1984). Some growth points in investigative plant ecology. *Trends in Ecological Research for the 1980s* (Ed. by J.H. Cooley & F.B. Golley), pp. 51–74. Plenum Press, New York.
- Grubb, P.J. & Edwards, P.J. (1982). Studies of mineral cycling in a montane rain forest in New Guinea. III. The distribution of mineral elements in the above-ground material. *Journal of Ecology*, 70, 623–648.
- Grubb, P.J., Flint, O.P. & Gregory, S.C. (1969). Preliminary observations on the mineral nutrition of epiphytic mosses. *Transactions of the British Bryological Society*, 5, 802–817.
- Harley, J.L. & Smith, S.E. (1983). *Mycorrhizal Symbiosis*. Academic Press, London.
- Hedberg, O. (1968). Taxonomic and ecological studies on the Afroalpine flora of Mt. Kenya. *Hochgebirgsforschung*, 1, 171–194.
- Hope, G.S. (1976). Vegetation. *The Equatorial Glaciers of New Guinea* (Ed. by G.S. Hope, J.A. Peterson, I. Allison & U. Radok), pp. 113–172. Balkema, Rotterdam.
- Huiskes, A.H.L. (1979). Biological Flora of the British Isles: *Ammophila arenaria* (L.) Link. *Journal of Ecology*, 363–382.
- Jarvis, P.G. & Jarvis, M.S. (1964). Growth rates of woody plants. *Physiologia Plantarum*, 17, 654–666.
- Jones, K., King, E. & Eastlick, M. (1974). Nitrogen fixation by free-living bacteria in the soil and in the canopy of Douglas Fir. *Annals of Botany, New Series*, 38, 765–772.
- Kohyama, T. (1984). Regeneration and coexistence of two *Abies* species dominating subalpine forests in central Japan. *Oecologia*, 62, 156–161.
- Lawrence, D.B. (1958). Glaciers and vegetation in southeastern Alaska. *American Scientist*, 46, 89–122.
- Lloyd, P.S. & Pigott, C.D. (1967). The influence of soil conditions on the course of succession on the chalk of southern England. *Journal of Ecology*, 55, 137–146.
- Lohmeyer, W. (1971). Über das Polygono-Chenopodietum in Westdeutschland unter besonderer Berücksichtigung seiner Vorkommen am Rhein und in Mündungsgebiet der Ahr. *Schriftenreihe Vegetationskunde, Bonn*, 5, 7–28.
- Nye, P.H. & Tinker, P.B. (1977). *Solute Movement in the Soil-Root System*. Blackwell Scientific Publications, Oxford.
- Orians, G.H. & Solbrig, O.T. (1977). A cost-income model of leaves and roots with special reference to arid and semi-arid areas. *American Naturalist*, 111, 677–690.
- Peace, W.J.H. & Grubb, P.J. (1982). Interaction of light and nutrient supply in the growth of *Impatiens parviflora*. *New Phytologist*, 90, 127–150.
- Pickett, S.T.A. (1980). Non-equilibrium coexistence of plants. *Bulletin of the Torrey Botanical Club*, 107, 238–248.
- Remmert, H. (1984). And now? Ecosystem research! *Trends in Ecological Research for the 1980s* (Ed. by J.H. Cooley & F.B. Golley), pp. 171–191. Plenum Press, New York.

- Richard, J.L. (1975). Dynamique de la végétation au bord du grand glacier d'Aletsch (Alpes suisses). *Sukzessionsforschung* (Ed. by W. Schmidt), pp. 189–206. Cramer, Vaduz.
- Rune, O. (1965). The mountain regions of Lappland. *Acta phytogeographica suecica*, **50**, 64–77.
- Sprent, J.I. & Thomas, R.J. (1984). Nitrogen nutrition of seedling grain legumes: some taxonomic, morphological and physiological constraints: opinion. *Plant, Cell and Environment*, **7**, 637–645.
- Stainton, J.D.A. (1972). *Forests of Nepal*. Murray, London.
- Taylor, P.E. (1982). *The development and ecological significance of mycorrhiza in contrasted groups of chalkland plants*. Ph.D. dissertation, University of Cambridge.
- Tüxen, R. (1975). Dauer-Pioniergesellschaften als Grenzfall der Initialgesellschaften. *Sukzessionsforschung* (Ed. by W. Schmidt), pp. 13–19. Cramer, Vaduz.
- Veblen, T.T. & Ashton, D.H. (1978). Catastrophic influences on the vegetation of the Valdivian Andes, Chile. *Vegetatio*, **36**, 149–167.
- Viereck, L.A. (1966). Plant succession and soil development on gravel outwash of the Muldrow Glacier, Alaska. *Ecological Monographs*, **36**, 181–199.
- Wardle, P. (1980). Primary succession in Westland National Park and its vicinity, New Zealand. *New Zealand Journal of Botany*, **18**, 221–232.
- Weatherell, J. (1957). The use of nurse species in the afforestation of upland heaths. *Quarterly Journal of Forestry*, **51**, 298–304.
- Wells, P.V. (1976). A climax index for broadleaf forest: an *n*-dimensional, ecomorphological model of succession. *Central Hardwood Forest Conference* (Ed. by J.S. Fralish, G.J. Weaver & R.C. Schlesinger), pp. 131–176. Department of Forestry, Southern Illinois University, Carbondale, Illinois.
- West, D.C., Shugart, H.H. & Botkin, D.B. (Eds) (1981). *Forest Succession: Concepts and Application*. Springer, New York.
- White, P.S. (1979). Pattern, process, and natural disturbance in vegetation. *Botanical Reviews*, **45**, 229–299.
- Whitmore, T.C. (1975). *Tropical Rain Forests of the Far East*. Clarendon, Oxford.